ANNUAL ACTIVITY PATTERNS OF CAGED NON-MIGRATORY WHITE-CROWNED SPARROWS

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NIGHT restlessness (locomotor activity) in caged night-migratory birds during the season of migration is generally equated with migratory restlessness (*Zugunruhe*) while caged non-migratory birds usually exhibit no such night restlessness (Farner, 1955). None was found in the House Sparrow (*Passer domesticus*) (Eyster, 1954) or the Clark Nutcracker (*Nucifraga columbiana*) (Farner and Mewaldt, 1953). On the other hand, Farner, King, and Wilson (1957) report vernal night restlessness in a non-migratory race of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). They state, however, that such activity was of relatively low intensity (13 per cent of total activity) compared to substantial night activity (51–69 per cent of total activity) in three migratory taxa of the same genus (*Z. leucophrys gambelii, Z. atricapilla,* and *Z. querula*). Mewaldt, Kibby, and Morton (1968) found that nocturnal activity, as a per cent of total activity, was lower in the non-migratory *Z. l. nuttalli* than in the closely related, but migratory, *pugetensis*.

Our objective is to characterize the relatively weak, but none-the-less present, night activity of this non-migratory race (*nuttalli*) of *Zonotrichia*. We have examined the circadian activity patterns and the orientation of day and night activity of several individuals over a period of more than a year. If night restlessness may be equated with an expression of migratory behavior in migratory birds, what is the significance of night restlessness in this non-migratory taxon?

MATERIALS AND METHODS

1. *Experimental Birds.*—Six immature male White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) were captured in June 1961 with Japanese mist nets near the mouth of the Pajaro River, Monterey County, California. From capture until this study began in December 1961 they were kept in Hendryx flight cages, in an outdoor aviary, on the roof of the Natural Sciences Building, San Jose State College, San Jose, California. During this time prior to our study they were used in a crown plucking experiment reported by Morton (1962). In addition, four adults which had been captured, banded, and released in June 1961 were recaptured in the same area in December 1961 and used for this investigation. Three were males; bird 843 was a female. Birds captured as immatures will consistently be referred to as immatures even though by the end of the experiment they were in adult plumage and over two years old.

Ground dry commercial dog food and water were provided ad libitum, and supplemented weekly with chick scratch, red millet, grit, and fresh lettuce. Once a week the birds were weighed and examined for molt. Molt readings were taken by examining the

retrices, body, crown, dorsal wing coverts, and remiges. Each bird was then rated as having no molt, or to be in light, medium, or heavy molt. These designations were then used in the following formula to provide a mean numerical index to the intensity of molt:

$$\text{Molt Index} = 10 \times \frac{(\text{no. light} \times 1) + (\text{no. medium} \times 2) + (\text{no. heavy} \times 3)}{\text{total number of birds}}$$

2. *Activity cages and recording apparatus.*—Two (864, 879) of the 10 birds were kept in reserve in a large walk-in cage. The others were placed in one of two kinds of cages we used in studying activity patterns. All cages were outdoors; however, the small cages were sheltered from wind and rain under an overhanging roof which permitted these birds to see a small portion of the sky.

Four birds (Adults, 843, 875; Immatures, 867, 869) were placed individually in small cages (41 × 22 × 26 cm) with a centrally located activity-sensitive perch, adapted from the design of Farner and Mewaldt (1953). Each time the bird depressed the centrally located perch, which extended across the width of the cage (22 cm), a microswitch was closed and an impulse sent to a recorder. The activity was monitored on four channels of a remotely located 20-pen, Esterline-Angus event recorder.

Four birds (Adults, 845, 850; Immatures, 840, 866) were placed individually in activity-orientation cages of the type used by Mewaldt and Rose (1960) and by Mewaldt, Morton, and Brown (1964). These circular cages were 94 cm in diameter and 15 cm high. A masonite screen 58 cm high and 152 cm in diameter surrounding each cage provided a homogenous circular horizon and screened off most of the local environment. However, the birds could see the top of a nearby tree and a small portion of the surface of the roof through the hardware cloth floor of the cage. Each cage had a central circular perch attached to the circular foodcup. Around the periphery of the cage were eight activity-sensitive perches each occupying just under 45 degrees of the 360 degree circle. For example, the activity in an easterly direction represents activity from 68° to 112° and was recorded on the appropriate channel on the Esterline-Angus tape. Activity on the four sets of eight perches was monitored by two remotely located 20-pen, Esterline-Angus recorders.

Continuous 24-hour activity recordings for an entire year were begun on the eight birds (four in activity cages and four in activity-orientation cages) in early December 1961. The birds were occasionally switched among the four single-perch activity cages to check for differences in the characteristics of perch-microswitch assemblies. No significant differences were detected. Although the four circular activity-orientation cages were also nearly identical the birds were occasionally switched from one cage to another to minimize the effects of any minor differences among the cages or the possibility of preference for or fixation on a particular perch.

3. *Analysis of data.*—Tapes in the Esterline-Angus recorders were run at three inches per hour. When a bird was very active, the ink marks ran together and the actual number of perch registrations could not be determined. For such times, each two-minute interval filled with pen marks was counted as fifteen perch registrations. This allowed a maximum count of 450 per hour. Experience with faster moving tapes, with direct observations, and with digital print-out recorders established that fifteen registrations for a two-minute interval was a conservative estimate. This interpretation appeared not to affect the circadian patterns of activity except to reduce the amplitude of peak activity periods.

Because we recorded approximately 111,000 bird-hours during the twenty months of the investigation on up to 36 channels simultaneously it was not practical to make actual

counts of all data obtained. Since the night activity was judged to be of greater interest, all night activity for the first 12 months was analyzed. Daytime activity was usually heavy and in the activity-orientation cages tended to be random, making data reduction more time consuming and, most likely, less rewarding. Therefore, day activity was sampled by counting perch registrations per hour only one day each week for each bird. Wednesday was chosen because it was well removed from the weekly disturbance of weighing done on Fridays or Saturdays. If there happened to be undue disturbances or recording troubles on a Wednesday, either Tuesday or Thursday was substituted as the "typical day" of the week.

For the period December 1961 through November 1962 circadian activity patterns were calculated for four birds. These consisted of one adult and one immature in the activity cages and for one in each age class in the activity-orientation cages. Data for these patterns by months consisted of the arithmetic means of each hour's locomotor activity for each of the four or five Wednesdays of each month.

In December 1962 we transferred the birds in the four activity-orientation cages to individual single-perch activity cages. These were placed next to the cages of the four birds that had been in the single-perch cages since December of 1961. We continued to monitor the circadian activity patterns of all 8 birds until the end of July 1963. Beginning in December 1962 locomotor activity of each of the eight birds was accumulated hourly on digital print-out recorders (Elmeg). During periods of intense activity, hourly counts of perch registrations on the Elmeg recorders exceeded the 450 arbitrary maximum on the Esterline-Angus recorders running at three inches per hour. We have attempted to equate graphically (Fig. 4) the quantitative aspects of locomotor activity monitored by the impulse markers (Esterline-Angus) and impulse counters (Elmeg).

Data from the eight peripheral perches of each activity-orientation cage were analyzed according to the method of Mewaldt, Morton, and Brown (1964). The mean azimuth is expressed in degrees from north. North equals 0°, east equals 90°, south equals 180°, and west equals 270°. These azimuths are presented plus or minus the angular deviation(s) in degrees, calculated according to Batschelet (1965) where $s = \sqrt{2(1-r)}$ in radians and $s = 57.296 \sqrt{2(1-r)}$ in degrees. ("Vector value" in the 1964 paper of Mewaldt, Morton, and Brown is equal to 100r.) Batschlet's "s" for circular distributions is roughly analogous to the standard deviation of a linear distribution.

We tested these circular distributions for randomness with an approximate test which we devised and which is independent of the total number of perch registrations in each distribution. We agree with Hamilton (1966) that the number of perch registrations is not the number of independent choices and thus should not be used as "N" in statistical determinations. Our test is similar in principle to that of Emlen (1967a and b) but much simplified. By taking the algebraic sums of the frequencies of the perch registrations in opposing directions starting with the direction with maximum frequency, we establish a situation where the theoretical line for randomness has both zero slope and zero origin. For the circular normal distribution the theoretical line for orientation is essentially a straight line with slope and origin significantly greater than zero. (In a badly skewed distribution only the origin exceeds zero.) For each distribution tested we calculated the slope and origin of the line described by the 4 points resulting from the summing of opposing directional frequencies. Using the method of Simpson, Roe, and Lewontin (1960:226) we tested for orientation by testing whether zero fell outside the 95 per cent confidence interval of either the slope or the origin.
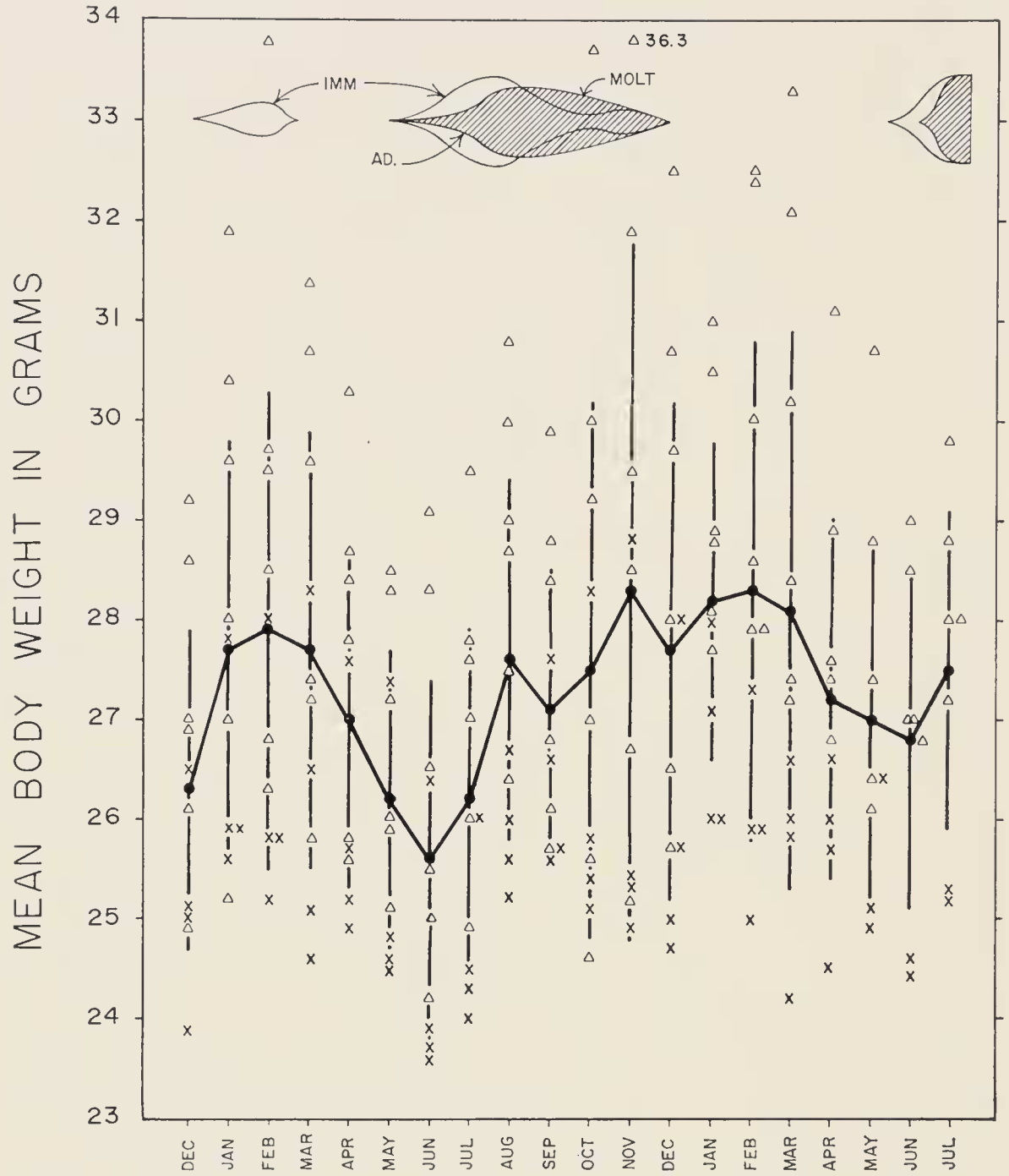
Fig. 1. Individual monthly mean body weights of four adults (x's) and six immature (Δ's) *Z. l. nuttalli*, December 1961 through July 1963. The large dark circles represent the combined means and the lines the standard deviations. Weekly means of body molt indices are represented graphically at the top of the figure.

BODY WEIGHT

Quite unexpectedly we found that the body weight of birds removed from their habitats as adults was consistently lower than that of those removed as immature birds (Fig. 1). This difference was not significant in individual months (e.g. $t = 1.706$, $d.f. = 8$ for March 1962, one of the times of greatest

variance). However, the 52 week mean weights of adults and immatures were significantly (barely) different at the 5 per cent level ($t = 2.3$, $d.f. = 8$). Data from the papers of Weise (1956), Odum and Perkinson (1951), and Blanchard (1941) and extensive data from our laboratory (including Mewaldt, Kibby, and Morton, 1968) indicate that male *Zonotrichia* are slightly larger than female *Zonotrichia*. The adult group consisted of three males and one female whereas the immature group consisted of six males. The lower weight of the single female in the adult group accounts for some of the low weights in the adult group. Although the rest of the differences probably represent a vagary of sampling, the consistently higher body weights of the immatures might suggest a favorable energy balance in these individuals.

Seasonal fluctuations were similar in the two groups; therefore, we have plotted (Fig. 1) the combined means. For both groups, highest weights were attained during the winter months and lowest weights during the spring and early summer. Similar seasonal fluctuations in body weight have been demonstrated for other species of birds (Nice, 1937; Baldwin and Kendeigh, 1938). It has been suggested that this seasonal cycle is correlated, roughly at least, with temperature, since individual birds usually gain weight during cold weather (provided adequate food is obtained) and lose weight during warm weather (Baldwin and Kendeigh, 1938). For our data, the correlation coefficient (r) of monthly mean weight and monthly mean temperature is −0.35, a definite, but small, negative correlation. This weight fluctuation should not be confused with the premigratory fat deposits of migratory birds. Odum and Perkinson (1951), working with migratory White-throated Sparrows (*Zonotrichia albicollis*), found that though changes in body lipids accounted for most seasonal changes in total body weight, the lean weight varied somewhat independently, being highest in the winter rather than spring. The increase in weight in July and August is probably due to the heavy annual molt and the subsequent high water content of the growing feathers. Odum and Perkinson (1951) found that molting birds had greater total weight, but lower lipid content than non-molting post-migratory birds.

MOLT

Some *nuttalli* exhibit a partial prenuptial molt beginning in late January and extending through February. When this molt occurs it is usually light and involves feathers of the crown and, to a lesser extent, those of the body (Blanchard, 1941; Mewaldt, Kibby, and Morton, 1968). In this study only the immatures exhibited this prenuptial molt with five out of six birds showing some molt during the first spring of the study (Fig. 1). These six birds showed no prenuptial molt in their second spring. No adults showed prenuptial molt. The postnuptial molt of the adults started later and was completed
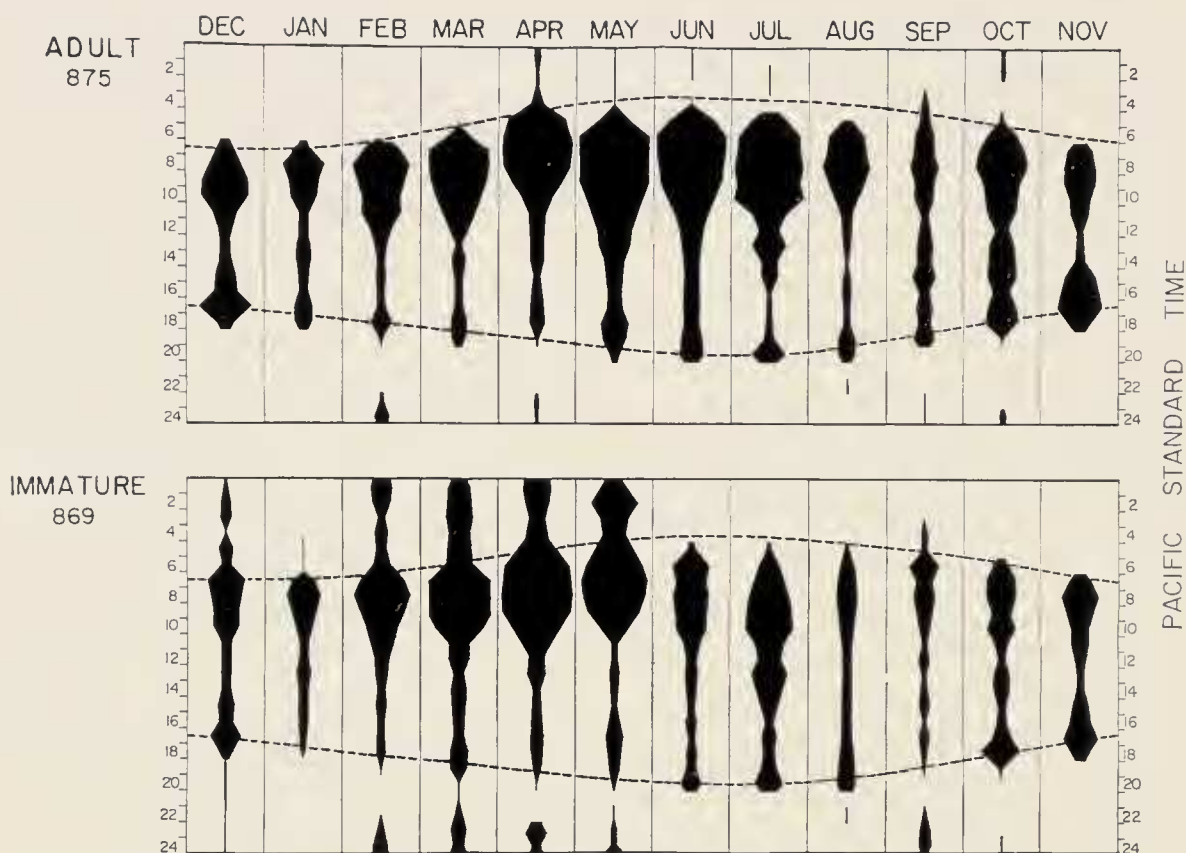
FIG. 2. Circadian patterns of an adult and an immature *Z. l. nuttalli* in activity cages. Dashed line indicates twilight. Full width of each month = 500 perch registrations per hour.

later than the postnuptial molt of the immatures. The six immatures began their first postnuptial molts between 9 June and 9 July. Between 3 and 17 August all six were in heavy molt. The four adults began their postnuptial molts between 16 June and 20 July and were all in medium or heavy molt between 17 August and 7 September. By 14 September all but one immature had completed the molt; however, the first adult to finish the molt did not do so until 14 October. The second summer only two of the original adults were still alive. They again started their molt a little later (Fig. 1) than the immature group which by now was about 2½ years old.

CIRCADIAN PATTERNS OF ACTIVITY

The data for the circadian activity patterns (Figs. 2 and 3) were obtained by taking the arithmetic means of the respective hours from the "typical days" for a given month. Each hour was plotted in the middle of the hour; e.g., the plot of the arithmetic mean for the eighth hour (08:00) is between 07:00 and 08:00. The birds generally showed high morning activity diminishing toward midday and exhibited another peak of lesser intensity at sunset. Many different bird activities follow this pattern: for example: feeding, nest
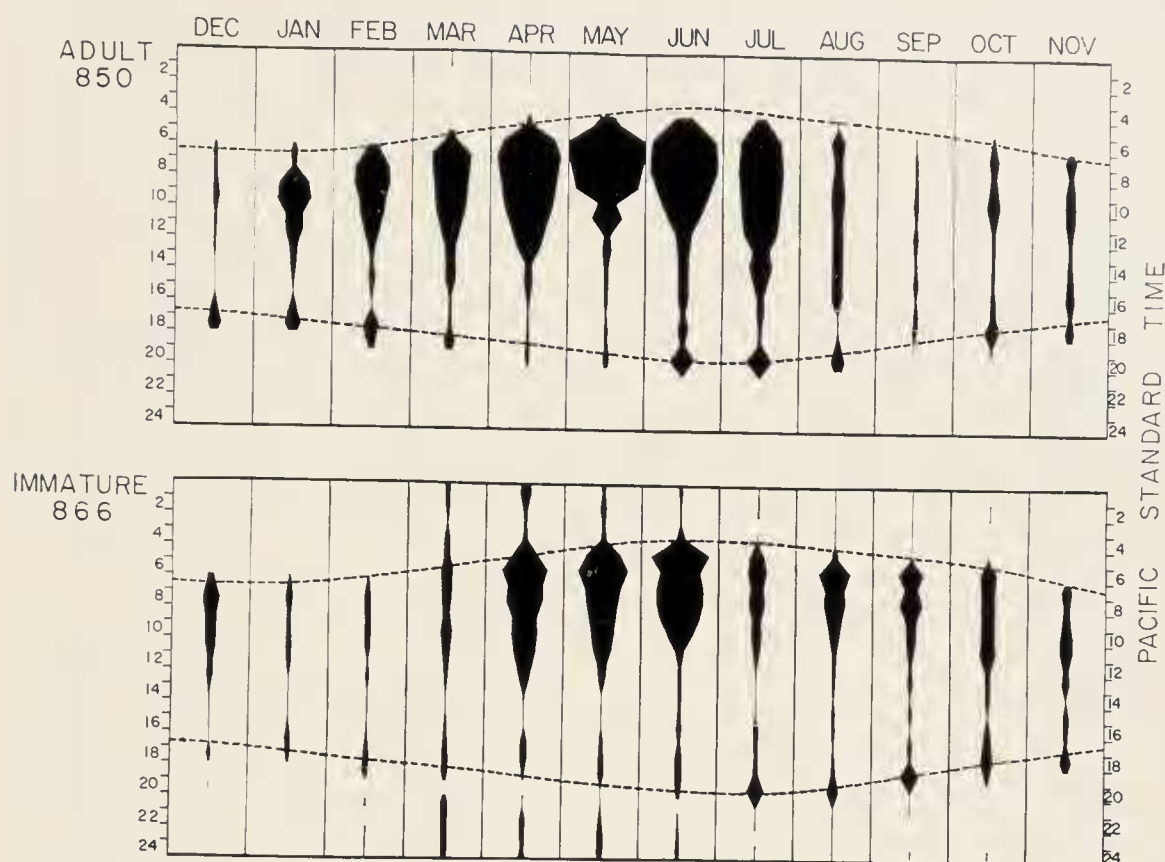
FIG. 3. Circadian patterns of an adult and an immature *Z. l. nuttalli* in activity-orientation cages. Dashed line indicates twilight. Full width of each month = 3000 perch registrations per hour.

building, and singing (Eyster, 1954). The evening peak is usually reduced or absent when the bird shows night activity (Palmgren, 1949; Mewaldt, Morton, and Brown, 1964.) It should be noted that no evening peak is shown for immature 869 in January (Fig. 2). This bird did display sporadic night activity during January but never on Wednesday—the arbitrary "typical" day. Also adult 850 (Fig. 3) lacks both morning and evening peaks in the month of September. This bird was in heavy molt in September and possibly the high energy demands of this molt resulted in reduced activity. Eyster (1954) reported a conspicuous decrease in the daily activity of the White-crowned Sparrow (*Z. l. leucophrys*) during molt.

Most of the night activity began several hours after sunset and continued on through the early morning hours until sunrise. There appeared to be a period of rest between sunset and the onset of nocturnal unrest. Eyster (1954) confirmed the results of other workers that, in migratory birds rest pauses usually occur before and after nocturnal activity during the migratory period.

Migratory *Zonotrichia*, which are night migrants, tend to exhibit less daytime activity in spring when they become active at night (*Zugunruhe*) (Eyster, 1954 and Mewaldt, Morton, and Brown, 1964). The unusually high
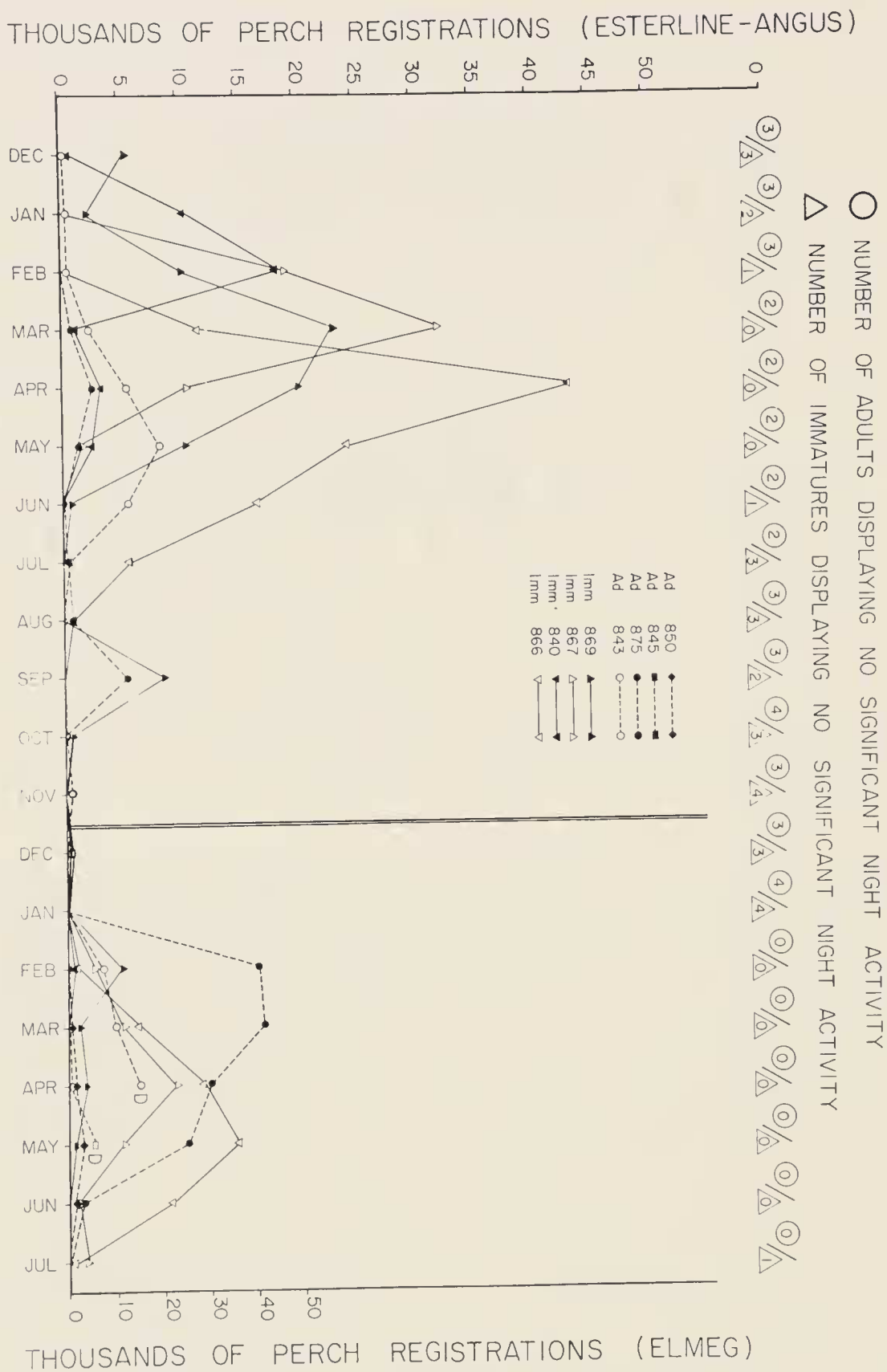
Fig. 4. Total night activity by months of four adult and four immature *Z. l. nuttalli.*
Ordinate change in December 1962 reflects change from ink-marking to digital counter
monitors for locomotor activity. Records of two birds were terminated by death (D)
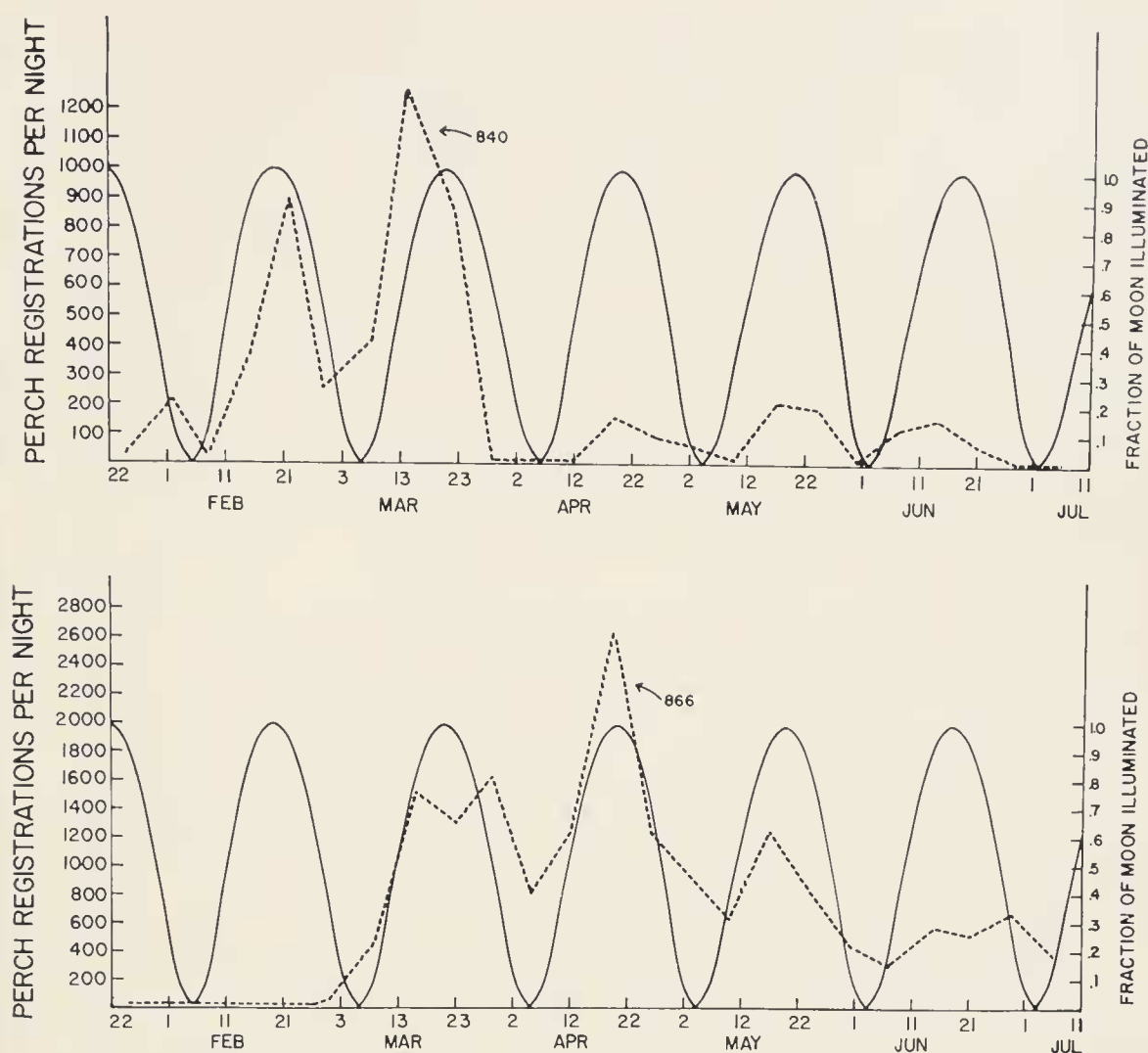in 1963.

FIG. 5. Moon influence on quantity of night activity of two immature *Z. l. nuttalli* in activity-orientation cages. Solid lines indicate the fraction of the moon's disk illuminated as a convenient index of the brightness of the moon.

morning locomotor activity exhibited by our non-migratory *nuttalli* in February and March is probably associated with the development of the gonads and may be equated with breeding activity. Blanchard (1941) reports that breeding behavior in *nuttalli* begins with establishment of territory in mid-January. The circadian activity patterns of our *nuttalli* were similar throughout the year and resemble those of non-migratory birds. However, when night activity was present the evening peak disappeared, a phenomenon characteristic of night migrants.

NIGHT ACTIVITY

The records of night activity for each night for all eight birds in recording cages for a year and a half are summarized by monthly totals (Fig. 4). The data for the first year (December 1961 to November 1962) were recorded

TABLE 1

NIGHT ACTIVITY OF ADULT *Z. L. NUTTALLI* IN ORIENTATION CAGES.

Bird Date	Fraction of Moon Illuminated	Activity Index	Mean Azimuth ± Angular Deviation
Bird #845			
May 18–19	0.99	49	91 ± 50
19–20	1.00	98	127 ± 36
20–21	0.98	18	127 ± 18
June 12–13	0.75	64	128 ± 58
		229	120 ± 47
Bird #850			
Mar. 26–27	0.72	124	35 ± 41
27–28	0.62	305	000 ± 45
Apr. 20–21	0.99	155	339 ± 40
21–22	0.96	62	341 ± 36
23–24	0.85	110	352 ± 27
May 03–04	0.00	39	333 ± 26
21–22	0.94	135	339 ± 26
		930	353 ± 41

by Esterline-Angus recorders and the data for the second year were recorded by Elmeg print-out counters. Counts obtained by the Elmeg counter were at least 2 to 2½ times greater during periods of peak activity than the counts obtained by our method of analyzing the Esterline-Angus data. Figure 4 represents this difference graphically.

During the first spring all four immatures (now nearly one year old) displayed substantially more night activity than any of the four adults. Whereas three immatures showed greatest night activity in March, one immature and the two adults, showing any significant night activity, reached peak activity in April and May.

The birds in the orientation cages were directly exposed to moonlight whenever the moon was approximately 25° or greater above the horizon. Since the night activity of migratory birds is sensitive to changes in light intensity (Wagner, 1957) we investigated the possible effect of moonlight on these birds' activity. We found (Fig. 5) that both of the immatures had a remarkably strong positive correlation of peaks of night activity with nights of bright moon. Moon brightness is presented as the fraction of the moon's disk illuminated (data from American Ephemeris and Nautical Almanac, U.S. Naval Observatory, 1962). The highest peaks of night activity are in the spring in both immatures; however, the maximum of bird 840 is one

month ahead of bird 866. The two adults in the orientation cages had a total of 11 nights when they had night activity, all but one of these nights occurred during a period of bright moonlight (see Table 1).

The birds in the small cages were partially sheltered from moonlight by an overhanging roof. However, they also showed peaks of activity coinciding with the full moon. Immature bird 869 had peaks of night activity which coincided with the full moons of February, March, and April. Immature bird 867 showed his first significant night activity in February as the moon began to increase in brightness. His peak of activity spanned the full moons of February and March and a smaller peak coincided with the full moon of April. Night activity was much less in the adults; however, a peak of activity of bird 843 was apparently related to the full moon of May and bird 875 had three small peaks of night activity related to the full moons of March, April, and May.

In the second spring (1963) the comparative amounts of activity exhibited by the original immatures and the adults were not separable. The two adults (875 and 843) again showed significant amounts of night activity but 875 showed relatively higher activity the second spring. Other than personal observation that this bird became increasingly nervous and cage worn as it remained in captivity, we cannot explain the high night activity of the second spring. The high amounts of activity exhibited by immature 866 in both years and the timing of its peak in April and May suggests that this individual bird possessed response characteristics of the migratory race *pugetensis* (Mewaldt, Kibby, and Morton, 1968). During the fall period only one adult and one immature showed appreciable night activity.

Most difference in vernal night activity between adults and the immatures disappeared the second spring probably because the immatures were in their second year and should by then be considered adults. The difference does not appear to result from the fact that our immatures were in captivity longer than the adults since most adults remained low the second year as well. The data for the fall period were collected when the immatures were in their second year. If the birds had been tested during their first fall period it is possible that we could have found night activity.

The overall picture of night activity, even among individuals of the same age and locality, is one of great variation. The only real consistencies are that the main onset of vernal night activity occurred in late January and early February and terminated with the annual molt which began in mid-June.

ORIENTATION OF ACTIVITY

Daytime orientation.—Because the orientation of daytime activity was very much alike in the four birds tested, data from one adult (850) and one
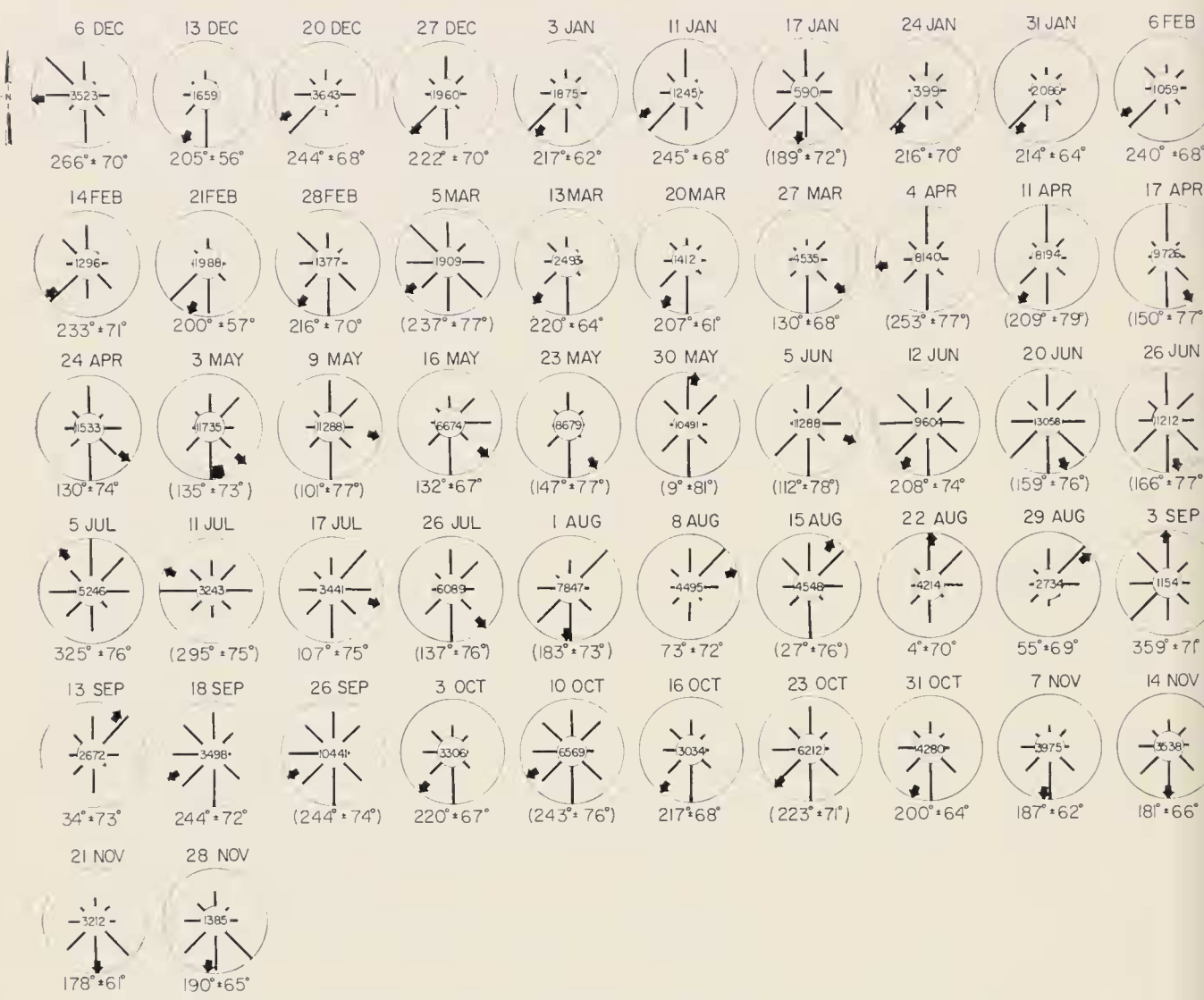
FIG. 6. The orientation of the daytime activity of an immature *Z. l. nuttalli*, bird 866. Number in circle is the total number of daytime perch registrations in "typical day." Arrow represents mean azimuth which is also presented beneath each circle with its angular deviation. Azimuths in parentheses were not significantly directed by our criterion.

immature (866) were examined in detail (Figs. 6 and 7). Angular deviations were generally high (maximum possible is 81). The 52 week mean angular deviation for adult 850 is 72 (SD ± 5.52) and for immature 866 it is 71 (SD ± 5.76). Over all, the day angular deviations of these two *Z. l. nuttalli* were higher than those of migratory *Zonotrichia* in similar experimental conditions (Fig. 8) indicating that the *Z. l. nuttalli* have less tendency than their migratory relatives to orient their day activity. These high angular deviations suggest very poor orientation and our test for randomness (see methods) confirms this conclusion by indicating that almost half of the days of each of these birds are not significantly directed (azimuths in parentheses in Figs. 6 and 7).

Fig. 7. The orientation of the daytime activity of an adult *Z. l. nuttalli*, bird 850. Number in circle is the total number of daytime perch registrations in "typical day." Arrow represents mean azimuth which is also presented beneath each circle with its angular deviation. Azimuths in parentheses were not significantly directed by our criterion.

Of those azimuths which were significantly directed, over 70 per cent in both birds fell in the range between 170° and 270°. This predominately southwest orientation might possibly be homing behavior since these birds were captured 40 miles almost directly south of San Jose. No homing ability has been previously reported for *Z. l. nuttalli*. Immature 866 was removed from its natal area well before it began its post-juvenal molt when it would normally have been imprinted with its home area (unpublished data in our laboratory); however, adult 850 might be expected to exhibit homing tendencies. We also examined the possibility that the birds' daytime orientation was related to a preference for the sunny or shady portions of the cage in relation to the time of day and/or the time of year. We found no progres-
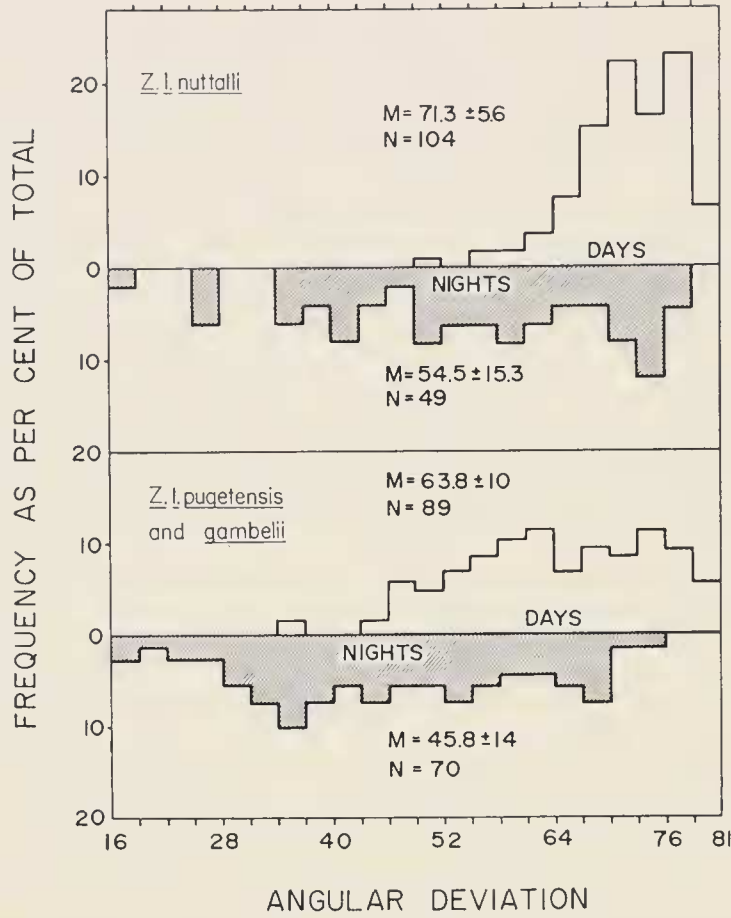
FIG. 8. Frequency distributions of day and night angular deviations on azimuths for *Z. l. nuttalli* (non-migratory) and *Z. l. pugetensis* and *gambelii* (migratory). All data included for *Z. l. nuttalli*. Data from two *Z. l. pugetensis* and two *Z. l. gambelii* under similar experimental conditions.

sive change in frequency of perch usage to correlate with the passage of the sun.

In April, May, and June adult 850 (Fig. 7) directed more activity to the north-northwest perches while continuing strong activity on the south perch. This change to a bimodal distribution of perch registrations was accompanied by a pronounced increase in daytime activity (Fig. 3) which persisted until the post-nuptial molt was well under way in late July. During the 8-week period from 6 February to 27 March, mean daily activity was 8,566 perch registrations with range from 4,713 to 10,334. Mean daily activity abruptly increased to 16,678 perch registrations with a range of 13,507 to 19,502 perch registrations per "typical" day during the 16-week period (5 April to 17 July). Because of the bimodal orientation during much of this 16-week period, angular deviations were high and in most of these weeks activity on the test day was random by our criterion. This does not, however, permit dismissal of possible functional significance of the persistent, if weak, change in direc-

tional choice during 16 weeks of very heavy activity coincident with the natural season of reproduction. Very little night activity was recorded for this bird during this, its first year in captivity. What night activity did occur, however, was significantly oriented north (see Table 1).

Behavior of immature 866 (Fig. 6) nearly paralleled that of adult 850. During April, May, and June, daytime activity was more than triple what it had been in the four previous months. Just prior to this increase in locomotor activity, the north perch was seldom used (13, 20, and 27 March). Coincident with the increase in day activity, the north perch was heavily used (4, 11, and 17 April), suggesting a carryover from night activity during those days. However, there was also considerable use of the perches in the north sector during August and September.

Nighttime orientation.—The adult birds in the activity-orientation cages showed little night activity. During the first spring, adult 850 was active only on the nights of 26 and 27 March, 20, 21, and 23 April, and 3 and 21 May (mean of perch registrations per night = 135) with a concentration of activity to the north (over-all angular deviation = 41) (Table 1). Adult 845 displayed night activity on 18, 19, and 20 May and on 12 June (mean of perch registrations per night = 56) with the activity oriented strongly to the southeast (over-all angular deviation = 47). The night activity of these two birds was strongly related to the presence of the moon and was of very low intensity; however, what little night activity each bird displayed was significantly oriented. The angular deviations compare favorably with those of the night activity of migratory *Zonotrichia* (Fig. 8). In both birds, night restlessness ocurred during the season when caged migratory *Zonotrichia* exhibit night restlessness (Mewaldt, Morton, and Brown, 1964). In neither case was the orientation phototaxic to the city lights, westerly in our experimental situation; however, the southeast orientation of bird 845 may have been phototaxic to the moon (see Brown and Mewaldt, 1968).

Immature 866 (Fig. 9) exhibited significant night activity during 22 weeks of the year. Its activity was oriented to the northwest beginning immediately after completion of the light prenuptial molt at the end of February. After four weeks it switched to a north-south pattern which persisted until the end of July. The angular deviations tend to be high (22 week mean = 66.1, SD ± 9.5) especially when the north-south components are nearly equal. This strong north-south tendency appeared even in the daytime activity (Fig. 6) during certain periods. Whenever this bird was disturbed for feeding, weighing, or cage cleaning it would rapidly jump from the perch to the floor, to the center perch and straight across to the opposite perch. These "across the cage" movements constituted a pattern of activity peculiar to this bird. When the data are analyzed, by the method employed here, the north and south

THE WILSON BULLETIN

4-10 DEC 11-17 DEC 18-24 DEC 25-31 DEC 1-7 JAN 8-14 JAN 15-21 JAN 22-28 JAN 29 JAN-4 FEB 5-11 FEB

12-18 FEB 19-25 FEB 26 FEB-4 MAR 5-11 MAR 12-18 MAR 19-25 MAR 26 MAR-1 APR 2-8 APR 9-15 APR 16-22 APR

(62) (511) (498) (286) (635) 828 1264 2654

309°±59° 324°±58° 330°±37° 316°±55° (48°±76°) 150°±73° 355°±61° (307°±77°)

23-29 APR 30 APR-6 MAY 7-13 MAY 14-20 MAY 21-27 MAY 28 MAY-3 JUN 4-10 JUN 11-17 JUN 18-24 JUN 25 JUN-1 J

(1237) (979) (643) (1252) (838) (454) (296) (578) (502) (666)

336°±71° 319°±72° 337°±61° 322°±55° 354°±71° 343°±67° 326°±73° 273°±75° 223°±73° (204°±74°

2-8 JUL 9-15 JUL 16-22 JUL 23-29 JUL 30 JUL-5 AUG 6-12 AUG 13-19 AUG 20-26 AUG 27 AUG-2 SEP 3-9 SEP

(412) (223) (156) (74) 8 21 39

241°±71° 232°±69° 315°±52° 355°±73°

10-16 SEP 17-23 SEP 24-30 SEP 1-7 OCT 8-14 OCT 15-21 OCT 22-28 OCT 29 OCT-4 NOV 5-11 NOV 12-18 NOV
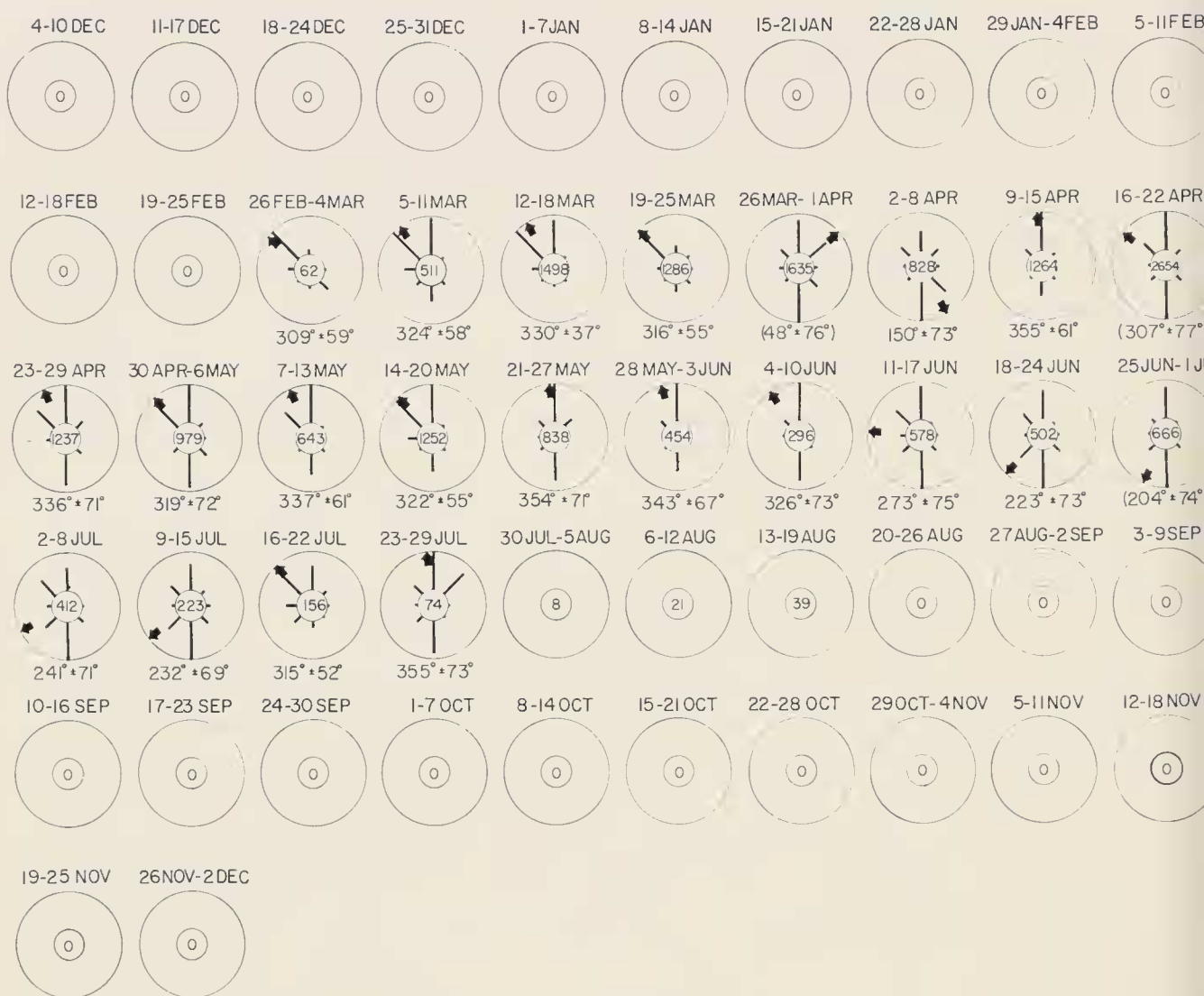
19-25 NOV 26 NOV-2 DEC

Fig. 9. The orientation of the night activity of an immature *Z. l. nuttalli*, bird 866. Number in circle is mean number of perch registrations per night. Arrow represents mean azimuth which is also presented beneath the circle with its angular deviation. Azimuths in parentheses were not significantly directed by our criterion.

components tend to cancel each other. Nevertheless, most week distributions were significantly directed by our criterion. The angular deviations do not reflect a true picture of what has occurred in this case. Such behavior is not without precedent; we have occasionally found "across the cage" responses in migratory *Zonotrichia*. Hamilton (1962) found alternation between north and south directional choices in two hand-reared Bobolinks. Lorenz and Tinbergen (1957) have indicated that organisms whose orienting responses have become stimulus-satiated often respond with an averting reaction to a previously positive stimulus. In spite of these bimodal distributions, the azimuths of bird 866 (Fig. 9) suggest that there was a greater tendency to orient toward the north than toward the south.
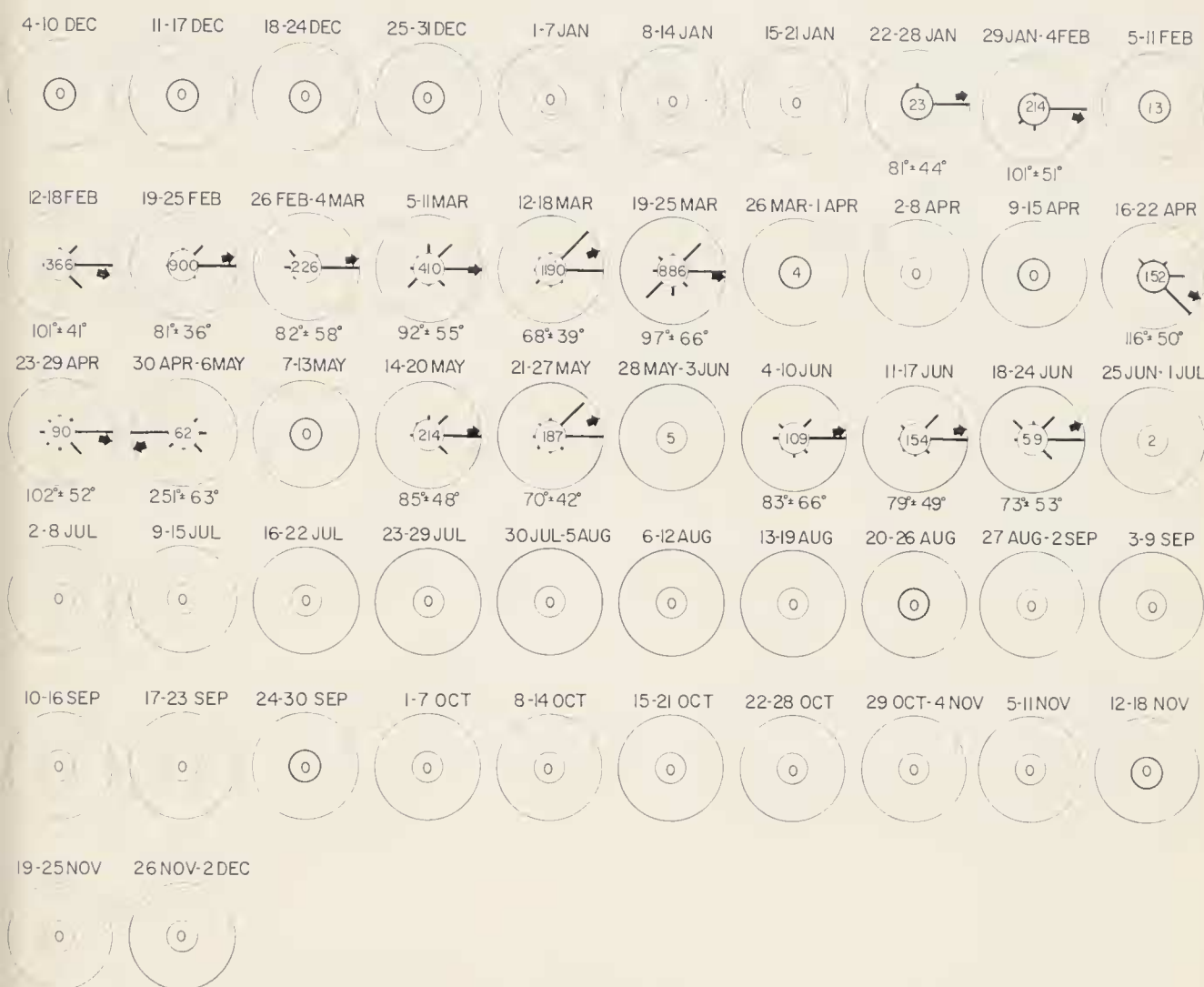
Fig. 10. The orientation of the night activity of an immature *Z. l. nuttalli*, bird 840. Number in circle is mean number of perch registrations per night. Arrow represents mean azimuth which is also presented beneath the circle with its angular deviation. All azimuths were significantly directed by our criteria.

City lights, visible to the birds as reflected light from clouds in the west on cloudy nights, did not seem to affect the northerly orientation of this bird. Likewise, the moon did not appear to influence the overall orientation of this bird. However, since most of its activity occurred during periods of bright moon, it is possible that some of its southward movements were phototaxic to the moon which is, of course, highest when it is due south. Night angular deviations sometimes increased during periods of bright noon. We propose that this bird was significantly orienting its night activity to the north. Closely related free-flying *Z. l. pugetensis* migrate to the north in late March and in April coincident with the period when this bird showed its greatest night activity. This bird (866) apparently possessed innate

atavistic migratory behavior which was appropriately expressed as northerly oriented nocturnal activity during the spring and early summer months. Persistence of nocturnal activity in caged migratory birds during the early summer months is characteristic (Merkel, 1958; Mewaldt, Morton, and Brown, 1964).

Beginning in late January, after a light prenuptial molt, immature 840 displayed sporadic night activity until mid-June (Fig. 10). This activity correlated strongly with the lunar cycle (Fig. 5). During 15 of the 16 weeks that the bird showed night activity it was strongly oriented to the east (mean angular deviation = 50.8, sd ± 8.93). The week of 30 April–6 May the bird was only active two nights and all of the orientation to the west occurred during one night. This primarily eastward orientation probably results only from the variation among individual birds. Mewaldt, Morton, and Brown (1964) found considerable spread of directional choices among migratory *Zonotrichia* in spring. It would be necessary to test many more individual *nuttalli* in order to determine the mean orientation azimuth for the taxon. The important thing is that these immature non-migratory birds had oriented night locomotor activity. In fact, their night locomotor activity is almost as strongly oriented as that of a representative group of migratory *Zonotrichia* under similar conditions (Fig. 8). In both the non-migratory birds and the migratory birds night angular deviations are more variable than day angular deviations and tend to be lower.

DISCUSSION

Matthews (1961) discussed the fact that two non-migratory taxons, *Anas platyrhynchos* and *Columba* sp. exhibited orientation when displaced geographically and released. He suggested that this orientation may function in keeping flocks together or in post-fledgling dispersal. It is possible that the night activity and orientation we have discovered in the non-migratory White-crowned Sparrow might also be related to post-fledgling dispersal. Dispersal of immature birds has been reported for many non-migratory species. Some examples are the Black-capped Chickadee (*Parus atricapillus*) (Odum, 1942), Pygmy Nuthatch (*Sita pygmaea*) (Norris, 1958), Wrentit (*Chamaea fasciata*) (Erickson, 1938), and the Song Sparrow (*Melospiza melodia*) (Johnston, 1956). Immature *nuttalli* flock after fledging but wandering may be confined to the period preceding the post-juvenal molt (Blanchard, 1941). Of 58 nestling *nuttalli* which were banded and success-fully fledged, only 12 were seen or reported after they had left their parents' territory. Eleven were seen within 400 yards of their birthplace during the nine months following fledging. Four of these eleven actually bred within 200–525 yards of their parents' territory. Remaining survivors, probably

numbering another dozen birds if we allow a 40 per cent survival, probably dispersed to a greater distance. This is suggested by the recovery (by shooting) of one bird the following spring 1½ miles from its birthplace. The post-fledgling dispersal of the Song Sparrow (*Melospiza melodia*), a very sedentary bird, was studied by Johnston (1956) and Nice (1937). Johnston found that only 10 per cent of the young sparrows moved to distances greater than 360 meters from their nests and that the direction of distribution was random when suitable habitat was available in all directions.

However, if the significantly oriented locomotor activity of *Z. l. nuttalli* were related to post-fledgling dispersal it seems unlikely that it would be exhibited in spring, occur at night, appear in adults, or be consistently oriented over a period of time. Because night activity peaks during the period of migration of the closely related migratory *Z. l. pugetensis*, we propose that the night activity and its orientation in *nuttalli* are atavistic remnants of an ancestral instinct to migrate. The non-migratory *nuttalli* are still in genetic contact with migratory *pugetensis* over a small geographic region from Westport to Capetown, California (Banks, 1964; Mewaldt, Kibby, and Morton, 1968). Certainly there is no doubt that spontaneous locomotor activity can have a genetic base since in rats it has been possible, by selective breeding, to initiate "active" and "inactive" strains with respect to spontaneous running activity (Rundquist, 1933; Brody, 1942 and 1950).

The display of night activity (= *Zugunruhe* ?) was weaker in the adult birds than in the immatures. It has been found in learning experiments that immature birds show more spontaneous activity than adults (Vince, 1961). Perhaps the establishment of territory by the adult further weakens an already vestigial instinct. It would be interesting to know if *nuttalli* are restless at night in their native habitat during the migratory season. Residents of San Francisco and Berkeley report that *nuttalli* commonly sing at night during the spring and summer months. Some suggest this "unrest" is caused by a relatively high incident light level from the city lights. Certainly our birds were much influenced by moonlight. Perhaps an innate tendency toward night restlessness is accentuated by conditions of capivity since the opportunity to expend energy is greatly lessened within the confines of a cage. The night activity of the immatures may be related to their higher body weights which suggest a favorable energy balance with more energy available to expend in activity.

Wagner (1930) states that "we recognize two extreme groups of birds; permanent residents which spend all of their life within a narrow range of their breeding grounds and migratory birds whose breeding grounds and wintering grounds are far apart. Between these two extremes there are various transition groups." The races of *Zonotrichia leucophrys* found in

central western California (*gambelii, pugetensis,* and *nuttalli*) represent all three of these categories to a certain extent. The strongly migratory *gambelii* might be placed at one extreme, whereas the "weaker" migratory *pugetensis* may represent a transitional stage. Although the *nuttalli* can be considered near Wagner's permanent resident extreme, individual birds apparently retain some characteristics of the transition group.

SUMMARY

We investigated body weight, molt, and locomotor activity of caged non-migratory White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) over a period of one and one half years including two springs. The four adults and six immatures used were captured in 1961 from the population which is permanently resident of the sand dune area near the mouth of the Pajaro River in Monterey County, California.

Locomotor activity patterns of two immatures (♂ ♂) and two adults (♂ and ♀) were continuously (24 hours per day) recorded in cages with single activity-sensitive perches from December 1961 to August 1963. The orientation of the locomotor activity of two imatures (♂ ♂) and two adults (♂ ♂), each in eight-perch activity-orientation cages, was monitored 24 hours per day from December 1961 to December 1962. In December 1962 these four birds were transferred to single-perch activity cages where their activity patterns were monitored until August 1963. Two additional immatures (♂ ♂) were held in a walk-in aviary. All ten were weighed and inspected for molt at weekly intervals. All birds were exposed to the natural weather at San Jose, California.

Body weight was inversely related to the mean environmental temperature. The weight of the fluids in the growing feathers probably accounted for an increase in weight in August. The mean body weight of the immatures was consistently, but not significantly, higher than the mean body weight of the adults in all months. Five of the six immatures showed a light prenuptial molt their first spring but not in their second spring. None of the four adults showed a prenuptial molt. The adults' postnuptial molt was about two weeks later than that of the immatures.

The circadian locomotor activity patterns of these birds displayed characteristic morning peaks and somewhat lesser evening peaks. The evening peaks were generally reduced or absent when the birds showed night activity. The morning peaks of activity increased greatly during the spring and early summer months. This increased restlessness during the day seems related to an increased availability of energy associated with a readiness to breed.

During the spring of 1962 all four immatures, but only two of the four adults, showed significant amounts of night locomotor activity. There was a remarkably strong positive correlation of peaks of night activity with nights of bright moon in all birds displaying night restlessness. The night activity of the two adults was of comparatively low intensity. In the fall only one adult and one immature showed night activity and that was very light in quantity. In the spring of 1963, by which time the original immatures were also adults, night activity levels of the two groups were broadly overlapping.

In the activity-orientation cages one immature showed a preference at night for north during the spring and summer months, whereas the other immature showed a definite preference at night for the east sector of the cage during the same period. No significant night activity was registered in the activity-orientation cages in the fall months. The very limited (less than ten nights combined) night activity of the two adults in activity-

oriented cages was none-the-less strongly oriented. The moon appeared to have little effect on the orientation of night activity, but it may have contributed to north-south "across the cage" movements in one bird. The angular deviations of both day and night activity compared favorably with those of migratory *Zonotrichia*. We propose the night restlessness of these non-migratory sparrows is a vestige of ancestral migratory behavior. The possible significance of weakly but frequently oriented daytime activity is also discussed. The possible importance of post-fledgling dispersal is discussed but judged to be unimportant in the behavior of these captive birds. It is possible that the quantity of night activity was somewhat influenced (presumably increased) by a surplus of metabolic energy incident to the restrictions of life in a cage.

ACKNOWLEDGMENTS

LITERATURE CITED

BALDWIN, S., AND S. KENDEIGH. 1938. Variations in bird weights. Auk, 55:416–467.

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow Zonotrichia leucophrys. Univ. California Publ. Zool., 70:1–123.

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. A.I.B.S., Washington, D. C.

BLANCHARD, B. D. 1941. The White-crowned Sparrows (Zonotrichia leucophrys) of the Pacific Seaboard: environment and annual cycle. Univ. California Publ. Zool., 46:1–178.

BRODY, E. G. 1942. Genetic basis of spontaneous activity in the albino rat. Comp. Psychol. Monogr., 17:1–24.

BRODY, E. G. 1950. A note on the genetic basis of spontaneous activity in the albino rat. J. Comp. Physiol. Psychol., 43:281–288.

BROWN, I. L., AND L. R. MEWALDT. 1968. Behavior of sparrows of the genus, Zonotrichia, in orientation cages during the lunar cycle. Z. Tierpsychol., 25:668–700.

EMLEN, S. T. 1967a Migratory orientation in the Indigo Bunting, Passerina cyanea Pt. I: Evidence for use of celestial cues. Auk, 84:309–342.

EMLEN, S. T. 1967b Migratory orientation in the Indigo Bunting, Passerina cyanea Pt. II: Mechanism of celestial orientation. Auk, 84:463–489.

ERICKSON, M. M. 1938. Territory, annual cycle, and numbers in a population of wrentits (Chamaea fasciata). Univ. California Publ. Zool., 42:247–334.

EYSTER, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. Ecol. Monogr., 24:1–28.

FARNER, D. S. 1955. The annual stimulus for migration: experimental and physiologic aspects. In Recent studies in avian biology (Wolfson, A., Ed.), Univ. Illinois Press, Urbana, pp. 198–237.

FARNER, D. S., AND L. R. MEWALDT. 1953. The recording of diurnal activity patterns in caged birds. Bird-Banding, 24:55–65.

FARNER, D. S., J. R. KING, AND A. C. WILSON. 1957. The development of vernal migratory behavior in caged individuals of several taxa of Zonotrichia. Anat. Rec., 128:546.

Hamilton, W. J., III. 1962. Bobolink migratory pathways and their experimental analysis under night skies. Auk, 79:208–233.

Hamilton, W. J., III. 1966. Analysis of bird navigation experiments. *In* Systems analysis in ecology. (Watt, Kenneth E. F., Ed.), Academic Press, New York.

Johnston, R. 1956. Population structure in Salt Marsh Song Sparrows, Part I. Environment and Annual Cycle. Condor, 58:24–44.

Lorenz, K., and N. Tinbergen. 1957. Taxis and instinctive action in the egg-retrieving behavior of the Greylag Goose. *In* Instinctive behavior. (Schiller, Claire H., Ed.), Internat. Universities Press, New York, pp. 178–208.

Matthews, G. V. T. 1961. "Nonsense" orientation in Mallard (*Anas platyrhynchos*) and its relation to experiments on bird navigation. Ibis, 103a:211–230.

Merkel, F. W. 1958. Untersuchungen über tages- und jahresperiodische Änderungen im Energiehaushalt gekäfigter Zugvögel. Z. vergl. Physiol., 41:154–178.

Mewaldt, L. R., S. Kibby, and M. L. Morton. 1968. Comparative biology of Pacific coastal White-crowned Sparrows. Condor, 70:14–30.

Mewaldt, L. R., M. L. Morton, and I. L. Brown. 1964. Orientation of migratory restlessness in *Zonotrichia*. Condor, 66:377–417.

Mewaldt, L. R., and R. C. Rose. 1960. Orientation of migratory restlessness in the White-crowned Sparrow. Science, 131:105–106.

Morton, M. L. 1962. A plucking experiment with White-crowned Sparrows. Condor, 64:327–328.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. I. Trans. Linnaean Soc., New York. 4.

Norris, R. A. 1958. Comparative biosystematics and life history of the nuthatches. Univ. California Publ. Zool., 56:119–300.

Odum, E. 1942. Annual cycle of the Black-capped Chickadee. Auk, 59:499–531.

Odum, E., and J. D. Perkinson, Jr. 1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory White-throated Sparrow. Physiol. Zool., 24:216–230.

Palmgren, P. 1949. On the diurnal rhythm of activity and rest in birds. Ibis, 91:561–576.

Rundquist, E. A. 1933. The inheritance of spontaneous activity in rats. J. Comp. Psychol., 16:415–438.

Simpson, G. G., A. Roe, and R. Lewontin. 1960. Quantitative zoology. Harcourt, Brace, New York.

U. S. Naval Observatory. 1962. American ephemeris and nautical almanac. Ephemeris for physical observations. U. S. Government Printing Office, Washington, D. C.

Vince, M. A. 1961. "String-pulling" in birds, III. The successful response in Greenfinches and canaries. Behaviour, 17:103–129.

Wagner, H. O. 1930. Über Jahres-und Tages rhythmus bei Zugvögeln. (I. Mitteilung) Z. vergl. Physiol., 12:703–724.

Wagner, H. O. 1957. The technical basis of experimental research on bird migration. Ibis, 99:191–195.

Weise, C. M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology, 37:274–287.

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